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Short running page heading: Tree-kangaroo hind limb muscular anatomy

Title: Anatomical adaptations of the hind limb musculature of tree-kangaroos for arboreal locomotion (Marsupialia: Macropodinae)

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Abstract

Tree-kangaroos (Dendrolagini) are Australasian marsupials that inhabit tropical forests of far northeastern Queensland and New Guinea. The secondary adaptation of tree-kangaroos to an arboreal lifestyle from a terrestrial heritage offers an excellent opportunity to study the adaptation of the musculoskeletal system for arboreal locomotion, particularly from a template well-adapted to terrestrial bipedal saltation. . We present a detailed descriptive study of the hind limb musculature of Lumholtz's tree-kangaroo (*D. lumholtzi*) in comparison to other macropodines to test whether the hind limb musculature of tree-kangaroos is functionally adapted to the different mechanical demands of locomotion in the uneven three-dimensional arboreal environment. The hind limb musculature of Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*), the western brush wallaby (*Macropus irma*), the western grey kangaroo (*Macropus fuliginosus*) and the quokka (*Setonix brachyurus*) are described. The hind limb anatomy of *D. lumholtzi* differed from that of the terrestrial macropodines in that the muscles had a greater degree of internal differentiation, relatively longer fleshy bellies and very short, stout tendons of insertion. There was also a modified arrangement of muscle origins and insertions that enhance mechanical advantage. Differences in the relative proportions of the hind limb muscle mass between tree-kangaroos and terrestrial macropodines reflect adaptation of the limb musculature of tree-kangaroos for arboreal locomotion. The hind limb musculature of *Setonix* was different to both *Dendrolagus* and *Macropus*, possibly reflecting its more basal phylogenetic position within the Macropodinae.

Key words: *Dendrolagus*, marsupial evolution, myology, *Setonix*

Introduction

Adaptation to an arboreal lifestyle has taken place in a number of mammalian groups including Primates, Carnivora, 'Insectivora', Rodentia, Xenarthra and various families of Marsupialia (Dublin 1903). The uneven and discontinuous nature of the arboreal realm imposes strong selective pressure on animals towards maintaining contact with the substrate,

maintaining balance, and providing propulsion on flexible, discontinuous and inclined branch substrates (Grand 1990). Small arboreal mammals (<3kg), including primates, have similarly flexed limb posture and movements which effectively lower the centre of mass for improved balance (Schmidt 2005a). Larger canopy-dwelling primates are often recognisable as being particularly acrobatic, and many demonstrate highly specialised use of the forelimbs for suspensory behaviours (Fleagle 1999). It has been noted, however, that primate morphology and locomotion are fundamentally different to other mammals and reflects forelimb adaptations in basal primates for locomotion on fine-branches (Jungers 1984; Schmitt and Lemelin 2002). Other large arboreal mammals, for examplesloth (*Bradypus* spp. and *Choloepus* spp.) binturong (*Arctictis binturong*) and koala (*Phascolarctos cinereus*), tend to move relatively slowly and deliberately, and employ prehensile digits and/or large, grasping claws to provide increased resistance to slipping and to help maintain contact with the substrate (Dublin 1903; Cartmill 1979; Grand 1990a; Argot 2001). A long, muscular, non-prehensile tail may be employed as a counter balance; or a prehensile tail may function as a grasping organ (Organ, Teaford *et al.* 2009; Organ 2010). On the whole, climbers are less muscular than runners, reflecting the reduced value of propulsive force as a function of branch compliance (Grand 1983; Grand 1990b). Instead, adaptations of the musculoskeletal system typically reflect enhanced flexibility of the joints for enhanced reaching and stepping movement, and improved mechanical advantage of limb adductor and digital flexor muscles to facilitate grasping of tree trunks or branches (Argot 2001). Further, a greater balance between pushing and pulling motions results in a trend towards a more even distribution of muscle mass between the fore- and hind-limbs in arboreal groups when compared to their terrestrial counterparts (Grand 1990b). Morphological variation between related species reflects the degree to which species inhabit the canopy (Dublin 1903).

Taxonomically, tree-kangaroos are placed within the marsupial subfamily Macropodinae, which includes kangaroos, wallabies and related taxa including the quokka (*Setonix brachyurus).* Tree-kangaroos evolved during the Late Miocene from a common ancestor with

rock-wallabies (Flannery 1989; Prideaux and Warburton 2010). Extinct plesiomorphic tree-kangaroos *Bohra* spp. have been described from a number of Pliocene and Pleistocene fossil deposits in Australia (Flannery and Szalay 1982; Dawson 2004; Hocknull 2005; Prideaux and Warburton 2008; Prideaux and Warburton 2009). There are ten species of extant tree-kangaroos (*Dendrolagus*) that are classified into two groups on the basis of morphology. The 'long-footed group' includes the two Australian species (*D. bennettianus* and *D. lumholtzi)*, together with *D. inustus* (of New Guinea); the remaining seven New Guinean species comprise the 'short-footed group' (Flannery 1989). The long-footed group of tree-kangaroos is apparently plesiomorphic, and thus likely to more closely approximate the hypothetical ground-dwelling ancestor (Grand 1990a; Flannery, Martin *et al.* 1996). Morphological variation within these groups (Warburton and Prideaux 2010) is likely to be tied to both phylogenetic and behavioural patterns, and for the short-footed group may reflect endemic species in highly localised regions of New Guinea (Flannery 1990). More detailed analysis of osteological differences between living and extinct species of tree-kangaroos will rely on investigations of the muscular anatomy of these species.

The musculoskeletal anatomy of Doria's tree-kangaroo (*D. dorianus*) was documented in an early monograph (Carlsson 1914). More recently, observations of captive and, occasionally, wild animals have highlighted specialised behaviours in comparison to terrestrial kangaroos. Tree-kangaroos utilise a wide variety of behaviours and locomotor patterns (Windsor and Dagg 1971; Procter-Gray and Ganslosser 1986), and have variable adaptations for manual dexterity and manipulation (Procter-Gray and Ganslosser 1986; Iwaniuk, Nelson *et al.* 1998). Grand (1990) summarised the principal adaptations of tree-kangaroos for improved stability and propulsion suited to arboreality. Tree-kangaroos have more equal length and muscle strength between limbs and limb segments than terrestrial kangaroos (Grand 1990a). Their feet are short and broad, more plantigrade in posture, and have roughened palmar and volar surfaces and enlarged, powerful claws for enhanced frictional resistance (Carlsson 1914). They also have a reduced lumbar length and decreased flare of the iliac crest. When moving

along branches, tree-kangaroos employ a modified low-speed, alternating gait (Windsor and Dagg 1971). *Dendrolagus* has a reduced proportion of muscle mass to total body weight (less than three-quarters of the muscle weight of kangaroos), reduced epaxial musculature, and more equal ratios of forelimb to hind limb muscle and bone in comparison to terrestrial macropods (Grand 1990). These adaptations to the muscular system reflect changes to the centre of gravity, strength-to-weight ratio and muscular actions through the body and are convergent with other slow-moving arboreal climbers (Grand 1990). Grand (1990) also noted that mobility of the shoulder and hip joints was enhanced in *Dendrolagus* spp., and that forearms, calves, paws, and feet were relatively heavier, although no empirical data were presented.

Previous studies have alluded to likely adaptations of the muscular system of tree-kangaroos for an arboreal lifestyle. While the overall distribution of muscle mass within the body is suggestive (Grand 1990), it does not allow interpretation of differences in muscular system function. We might expect, for example, differences in the muscular attachments to improve mechanical advantage or manoeuvrability for locomotion in an arboreal setting. Here we present a detailed descriptive study of the hind limb musculature of Lumholtz's tree-kangaroo (*D. lumholtzi*) in comparison to other macropods to test whether the hind limb musculature of tree-kangaroos is functionally adapted to the different mechanical demands of locomotion in the uneven three-dimensional arboreal environment. To this end, we undertook to answer the following questions: 1) what is the anatomical arrangement of the hind limb muscles of Lumholtz's tree-kangaroo, 2) how does arrangement of the muscles compare with that of terrestrial taxa of the subfamily Macropodinae with respect to the bony attachments and distribution of muscle mass within functional muscle groups, and 3) to what extent do the differences observed between species reflect functional adaptations for climbing in tree-kangaroos? This information was then used to elucidate some of the functional patterns observed in the osteology of living and extinct tree-kangaroos.

Materials and Methods

An adult male road-killed specimen of Lumholtz's tree-kangaroo *Dendrolagus lumholtzi* from the Atherton Tableland region was made available for dissection by the Environmental Protection Authority, Queensland. Although this species is reportedly common in suitable habitat (Winter, Burnett *et al.* 2008)few specimens are collected and made available for anatomical dissection. Thus, this study is based on the dissection of only one specimen. However, in our experience, differences between species are generally greater than the variation observed within (e.g., Harvey and Warburton, 2010). The specimen was skinned, eviscerated and embalmed in 10% formalin 4% glycerol solution for one week, before being stored in 70% ethanol. Standard dissecting techniques were used. Muscles were identified and their attachments recorded. Muscle actions were determined by observation of the arrangement of the muscle fibres in relation to their position of origin and insertion relative to the bony articulation across which their pass.

Descriptions of macropod musculature found in the published literature were supplemented with our own new dissections and descriptions of the western grey kangaroo (*Macropus fuliginosus*), the western brush wallaby (*M. irma*) and the quokka (*Setonix brachyurus*). One specimen of each species was obtained for dissection: *M. fuliginous* purchased from King River International abattoir, Canning Vale WA; *M. irma* and *S. brachyurus* were collected as victims of road-incidents and donated for study by Western Australian Department of Environment and Conservation. These specimens were dissected fresh, following thawing and the muscle attachments were recorded.

The following published accounts of macropod musculature reviewed for comparative interpretation: *Aepyprymnus rufescens* (Lodder 1991), *Dendrolagus dorianus* (Carlsson 1914), *Hypsiprymnodon moschatus* (Carlsson 1915), *Macropus* spp. (Windle and Parsons 1898; Elftman 1929; Badoux 1965; Hopwood and Butterfield 1976; Hopwood and Butterfield 1990; Lodder 1991; Bishop 1997) and *Petrogale xanthopus* (Parsons 1896).

Results

Extrinsic muscles of the pelvic limb

M. iliacus arose from the iliac fossa on the entire ventral aspect of the body of the ilium (Figs 1A, 2B). M. psoas major originated from the ventral surface of the body and the transverse processes of the last three lumbar vertebrae. The two muscles joined at the level of the acetabulum to insert together to the lesser trochanter of the femur and medial aspect of the neck of the femur (Fig 3C). Together these muscles act to flex the hip joint. The bony attachments of the iliopsoas appear similar throughout the macropods we observed (*M. irma, M. fuliginosus, S. brachyurus*) and also in the literature (Hopwood & Butterfield 1976).

Gluteal region

M. gluteus superficialis (m. gluteus maximus) originated from the thick lumbar fascia adjacent to the dorso-medial border of the ilium and inserted to the caudal aspect of the greater trochanter, and proximal fascia of the biceps (Figs 2A, 3B, C). A small, additional portion inserted into the proximo-caudal fascia of the M. vastus lateralis. This muscle would act as an extensor and abductor of the hip joint. In *M. irma* the origin included a portion from the crest of the ilium, together with the gluteofemoralis, in addition to the thoracolumbar fascia, and the insertion included a strong aponeurotic connection to the fascia of the vastus lateralis at the position of the caudo-lateral aspect of the greater trochanter of the femur. As in *M. giganteus* (Hopwood and Butterfield 1976), fibres of the gluteofemoralis blended with the superficial gluteal. In *S. brachyurus*, the origin was from the thoracolumbar fascia only.

M. gluteofemoralis (m. caudofemoralis, m. femorococcygeus, m. agitator caudae)

M. gluteofemoralis comprised three distinct portions; a large superficial portion, had the most caudal origin from the transverse processes of the third and fourth caudal vertebrae; the middle portion (incompletely separable into two heads) from the transverse processes of the

third caudal vertebrae and from the deep caudolumbar fascia; and the third small, deep portion from the deep lumbar fascia together with the superficial gluteal muscle. Each fleshy belly gave rise to a tendon halfway along the length of the femur which converged to insert laterally to the capsule of the knee and proximo-lateral aspect of the patelloid (Fig 2A). The small, deep most cranial portion lay on the deep surface of the middle portion and had a common tendon. The gluteofemoralis functions to abduct femur and extend the hip joint.

The gluteofemoralis was more differentiated in *D. lumholtzi* with three distinct portions rather than the usual two. In *M. irma* the cranial portion had a broad origin from the crest of the ilium and the thoraco-lumbar fascia, together with the superficial gluteal. The caudal portion was very long from the caudolumbar fascia and the transverse process of the caudal vertebrae III, IV. The tendons united two-thirds of the length of the femur and insert together to patelloid. The insertion extends more distally in *D. lumholtzi* than in other macropodine taxa. In *M. fuliginosus* caudal head originated from the caudal vertebral transverse processes III, IV and V; the cranial head was very difficult to separate from the superficial gluteus at the origin. A small, incompletely separable portion was observed lying between the cranial and caudal heads, originating with the cranial head from the crest of the ilium. Lodder (1991) described cranial and caudal heads in *Aepyprymnus* and *M. giganteus*, as did Hopwood and Butterfield (1976). The cranial head appeared relatively larger in *M. fuliginosus* than in *M. irma*. In *S. brachyurus* there was no origin from the ilium. Carlsson (1915) describes two distinct portions (m. femorococcygeus and m. caudofemoralis) which apparently have a more proximal origin in *H. moschatus* .

M. gluteus medius

M. gluteus medius had two large and distinct portions (Figs 1, 2A). The superior, caudal portion extended along lateral border of the ilium from the iliac crest to the caudal dorsal iliac spine. The inferior, cranial portion originated from the crest of the ilium and gluteal fascia. The cranial head inserted to the cranial aspect of the greater trochanter; the caudal portion

inserted to the caudolateral aspect of the greater trochanter by a strong, tendinous fibres (Figs 3A, B, C). This muscle acts to extend the hip joint.

In *D. lumholtzi* the two portions of the gluteus medius were very distinct; the large portion of the deep gluteal muscle laid between the two portions of the gluteus medius (Figs 1A, B). In *M. irma* two portions were present; a large, thick portion from the tuberosity of the ilium and a thinner caudal portion from along the dorsolateral crest of the ilium. Both portions inserted over the proximal aspect of the greater trochanter of the femur. Two portions have also been described for *M. giganteus* (Hopwood & Butterfield 1976) and *Petrogale* (Parsons 1896). Carlsson (1915) suggested that the middle gluteal was often arranged in two layers within marsupials, but not in *H. moschatus*. In *S. brachyurus*, the two portions were not separable from one another.

M. gluteus profundus

M. gluteus profundus was a very large muscle from the large gluteal fossa covering the lateral aspect of the wing of the ilium (Figs 1A, B). It had a strong insertion with superficial tendinous fibres and deep fleshy fibres to the proximal crest greater trochanter (Figs 3A, B, C). This muscle acts to extend the hip joint.

In *S. brachyurus* the origin was similarly from most of the elongate gluteal fossa. In *M. irma* the origin was more lateral along the wing of the ilium, and this insertion more medial on the greater trochanter. *M. fuliginosus* had an additional insertion with fleshy fibres to the medial aspect of the greater trochanter.

M. gluteus minimus

M. gluteus minimus was a small muscle from a triangular section at the base gluteal fossa of the ilium, in the quarter proximal to the acetabulum (Figs 1A, B). Insertion to the craniolateral base of the greater trochanter (Fig 3A). This muscle contributes to extension of the hip joint.

In *M. irma*, *M. fuliginosus* and *S. brachyurus* the origin was much more extensive, from the base of the ilium and along the entire lateral edge, along side the gluteal fossa. In each species the insertion was longer than in *D. lumholtzi*, along an arc from the craniomedial aspect and along the craniolateral line of the greater trochanter. The gluteal muscles as a group are apparently less specialised in *H. moschatus* (Carlsson 1915).

M. piriformis

M. piriformis arose from the transverse process of the first and second caudal vertebrae (Fig. 2B) and inserted proximally into the trochanteric fossa (Fig 3C). This muscle acts to extend and abduct the femur at the hip joint.

In *M. fuliginosus* and *M. irma*, the insertion was also to the crest of the greater trochanter, immediately proximal to the intertrochanteric fossa. We observed an additional very small slip of muscle adjacent to the piriformis from the transverse process of the second caudal vertebra which inserted to the mid-caudal tubercle of the femur, however, we are unable to attribute a formal name to this portion.

M. obturatorius internus

M. obturatorius internus originated from the dorsal portion of the medial face of the ischium and inserted into the middle portion of the trochanteric fossa of the femur together with the m. gemelli (Figs 2B, 3C). This muscle laterally rotates the femur and may also contribute to abduction at the hip joint.

The origin does not completely surround the obturator foramen in *D. lumholtzi*. The muscle appeared to be relatively small. The broad, flat tendon lies on the surface of the cranial gemellus; it was not separable from the cranial gemellus. A similar description of the obturator internus was given for *Petrogale* (Parsons 1896) and *M. giganteus* (Hopwood &

Butterfield 1976); the latter authors summarised that this muscle is generally reduced in size in marsupials, including macropods, in comparison to other mammals.

Mm. gemelli

Mm. gemelli comprised two adjacent portions from a large area on the lateral aspect of the ischium, between the acetabulum and the ischiatic tuberosity (Fig 1A). The insertion was to the trochanteric fossa of the femur, distal to the insertion of the m. piriformis; immediately proximal to the insertion of the external obturator muscle (Fig 3C). This muscle medially rotates and abducts the femur at the hip joint.

In *M. irma* the ilium was relatively longer, thus the muscle appeared larger. In *S. brachyurus*, the caudal belly extended onto the medial aspect of the ischiatic table.

M. quadratus femoris (m. ischiofemoralis)

M. quadratus femoris had a long, thin origin along the caudal aspect of the ischium, adjacent to the border of the ischium, from the lateral angle of the ischiatic tuberosity and along the ischiatic arch toward the pelvic symphysis (Fig 1A). The muscle inserted to the mid-caudal tubercle on the femoral shaft (Fig 3C). This muscle functions as a strong extensor of the hip joint and appeared to be relatively much larger in *D. lumholtzi* in comparison to the other species examined.

In *M. irma* and *S. brachyurus* the origin was triangular in shape, filling much of the lateral aspect of the ischiatic table; a triangular, raised fossa was observed on the bone. Hopwood and Butterfield (1976) reported that this muscle was mostly tendinous in *M. giganteus* to prevent hyperextension of the hip joint. The insertion is more proximal in *H. moschatus* to the greater trochanter (Carlsson 1915).

Cranial thigh

M. sartorius

M. sartorius originated from the cranioventral iliac spine (tuber coxae) (Figs 1A, 2A, B). The insertion was to the cranial aspect of the fascia of the knee and patelloid (Figs 2A, B). This muscle flexes the hip and extends the knee.

This strap muscle, with triangular section was incompletely separable into two portions, was similar in all macropod species examined.

Mm. quadriceps femoris

The four muscle of the quadriceps group function to extend the knee; the m. rectus femoris also acts to flex the hip. M. rectus femoris arose from the enlarged rectus tubercle on the lateral aspect of the ilium, cranial to the acetabulum (Figs 1A, 2B) and inserted to the cranial border of the patelloid. M. vastus lateralis originated from the cranial, lateral and caudal aspects of the base of the greater trochanter and proximal shaft of the femur (Figs 2A, B, 3A, B, C) and inserted to the lateral aspect of the proximal border of the patelloid. M. vastus medialis originated from the cranial aspect of the neck of the femur (Fig 3A) and inserted to the medial border of the patelloid. M. vastus intermedius was a very deep muscle along the surface of the femur, not clearly separable from the medial vastus. Its origin was from the craniomedial, cranial and craniolateral surface of the mid three-fifths of the shaft of the femur (Fig 3A) and it inserted to the craniolateral border of the patelloid.

All four bellies of the quadriceps femoris are closely attached; the three vasti share aponeuroses along their adjacent borders. In *S. brachyurus*, the origin of the vastus lateralis was thinner along the cranial, lateral and caudal aspects of the epiphyseal line of the greater trochanter. Origin of the vastus lateralis in *M. irma* was from the caudal aspect of the greater tubercle only. *M. fuliginosus* had a larger origin from the lateral surface of the greater trochanter. In *M. fuliginosu*s the rectus femoris was very thick and incompletely separable into two portions by the presence of a very strong internal aponeurosis. A single head was

observed in *M. giganteus* (Hopwood & Butterfield 1976); Parsons (1896) reported two heads for this muscle in *Petrogale*. Overall, the quadriceps muscle group, and especially the vastus lateralis muscle appeared to be relatively smaller in *D. lumholtzi* than in the species of *Macropus* dissected here.

M. tensor of the fasciae latae

M. tensor of the fascia latae was a short, thick, triangular muscle belly from the thoracolumbar fascia (Figs 2B, 4). It inserted to the deep, cranio-medial fascia of the quadriceps. This muscle is a tensor of the deep cranial fascia of the thigh, and thus contributes to extension of the knee.

In *M. irma*, *M. fuligniosus* and *S. brachyurus* origin extended along to the ilium, from the iliac spine to the proximal to the rectus tubercle, and inserted onto the fascia of the vastus medialis.

Medial thigh

M. pectineus

M. pectineus arose from the iliopubic eminence and triangular area of the pubic ramus medial to acetabulum (Fig 1A). The thin insertion was along medial aspect of middle half of femur (Fig 3A).Pectineus contributes to adduction and lateral rotation of the femur at the hip joint.

In *M. irma*, the origin was smaller in area, from the more distinct and protuberant iliopubic eminence. The extent of the insertion along the caudal aspect of the femur varied. In *M. irma* to the medial edge of the mid-caudal rugosity and distally along the medial shaft. In *M. fuliginosus* the insertion is to the proximal third of the medial shaft of the femur. In *M. giganteus* (Hopwood & Butterfield 1976) there was both a fleshy attachment on the proximal third of the femur and an aponeurosis for the two distal thirds. In *S. brachyurus* the insertion was to the proximal one-fifth of the medial femur, immediately distal to the third trochanter.

M. gracilis

M. gracilis took an aponeurotic origin along the length of the pelvic symphysis, and fleshy fibres from the caudal symphyseal tubercle (Fig 1A). The flat, aponeurotic insertion was to the medial surface superficial fascia of the crus at the level of the tibial crest (Fig 4). The gracilis muscle acts as an adductor of the thigh.

The gracilis was relatively thick in *D. lumholtzi*. In *M. irma* and *S. brachyurus* the origin extended laterally along the ischiatic arch. Division into two heads was observed in *M. fuliginosus*, as previously described for *M. giganteus* (Hopwood & Butterfield 1976). We did not observe an origin from the epipubic bone, as described for *M. giganteus* (Hopwood & Butterfield 1976). The origin is apparently more caudally restricted in *H. moschatus* (Carlsson 1915).

Mm. adductores (M. adductor longus, M. adductor brevis, M. adductor magnus)

Mm. adductores arose in two portions from caudal border of the ischium and from along the pubic symphysis (*m. adductor magnus et brevis*) (Figs 1A, 4). An additional small triangular portion (*m. adductor longus*) had an aponeurotic origin from the pubis together with the pubic portion above. The insertion was in three portions to the caudal aspect of the femur (Figs 3B, C). The adductor longus inserted immediately distal the trochanteric fossa; the pubic portion inserted to middle half of the caudal aspect of the femur; ischiatic portion to the distal fifth of distal medial aspect of the femur, immediately proximal to the intercondylar groove. This muscle group strongly adducts the femur at the hip joint.

In *M. irma* the origin was from the ventral surface of the pubis from the iliopectineal eminence to the ilium and ventral surface of two thirds of the greater ischiatic arch and including the mid-pubic tubercle. In *M. fuliginosus* the combined adductor mass (difficult to completely separate into portions) inserts to the entire medial surface of the femoral shaft. The insertion of the pectineus muscle separated the two portions of the adductor in *M. irma*

but not in *M. fuliginosus*. *S. brachyurus* had a similar arrangement to *M. irma*. During dissection, the adductor muscle mass appeared to be relatively large in *D. lumholtzi* in comparison to *M. fuliginosus* and *M. irma.*

M. obturatorius externus

M. obturatorius externus was a very large, thick muscle which encircled the ventral aspect of the obturator foramen, and extended over a large surface of the caudolateral ischium and pubis. It inserted deeply into the distal trochanteric fossa of the femur. The external obturator is a lateral rotator of the femur at the hip joint. This muscle appeared to be relatively very large in the tree-kangaroo. The insertion was closely associated with the tendons of the mm. gemelli.

Caudal thigh

M. biceps femoris

M. biceps femoris passes from the lateral tip of the ischiatic tuberosity and the fascia covering the semitendinosus to insert to the lateral fascia of the knee and crus covering the proximal third of the tibia (Figs 1A, 2A). The biceps femoris functions to abduct and extend the femur at the hip joint and extend the knee during the supporting phase (when the limb is weight-bearing). During the swing phase (non-weight-bearing) this muscle contributes to flexion of the knee.

In *D. lumholtzi* the two heads of the biceps femoris were incompletely separable. In *M. irma* the large, thick cranial head arose dorsally from the ischiatic tuberosity, the sacrotuberous ligament and fascia lata; the caudal head arose laterally from the ischial tuberosity. The cranial portion was inserted laterally to patelloid and crural fascia and the caudal portion inserted to crural fascia over gastrocnemius; the fascia continued distally to the common calcaneal tendon. The two portions were contiguous along their margin and were very strongly attached to the semitendinosus at their origin. The bony attachments were similar in

S. brachyurus. In *M. fuliginosus* the attachment between the biceps and the semitendinosus was not as strong as in *M. irma.* In *M. giganteus* the origin was from the tuber ischii (Hopwood & Butterfield 1976). Parsons (1896) noted additional origins from the sacrum and caudal vertebrae in *Petrogale.*

M. abductor cruris caudalis (m. tenuissimus)

M. abductor cruris caudalis arose from the proximal third lateral fascia of the semitendinosus. The insertion was to the lateral fascia of the crus, over the gastrocnemius, immediately distal to the insertion of the m. biceps femoris. The caudal crural abductor contributes to extend the thigh at the hip joint; it may also flex the knee joint.

M. semitendinosus

M. semitendinosus originated from the caudo-ventral aspect of the ischiatic tuberosity (Figs 1A, B, 2A, B, 4). The muscle crossed the caudal superficial aspect of the thigh and inserted into the deep medial crural fascia, from the level of the distal end of the tibial crest and covering a distance approximately one fifth of the length of the tibia. The fascia continued distally to contribute to the common calcaneal tuberosity. The semitendinosus functions for extension of the hip and knee joints, and, in non-weight bearing limb, flexion of the knee joint.

M. semimembranosus

M. semimembranosus arose from the middle half of the ischiatic arch (Figs 1A, 2B). The muscle was incompletely separable into two portions. The cranial head was inserted to the medial condyle of the tibia. The caudal head was inserted to the proximo-medial aspect of the superficial fascia of the crus and proximal end of the medial border of the tibia, at the level of the tibial crest. The semimembranosus contributes to extension of the hip and knee joints.

The slightly thicker cranial portion of the semimembranosus lies along the caudal aspect of the adductor, and is very difficult to separate. In the terrestrial macropodine taxa the origin was limited to the middle third of the ischiatic arch. In *M. fuliginosus* an additional insertion was observed to the medial epicondyle of the femur and the medial face of the tibia immediately below the condyle of the tibia.

Cranial leg

M. tibialis cranialis

M. tibialis cranialis arose from the cranial tibial crest and proximal lateral fossa of the tibia immediately distal to the lateral tibial condyle; proximal third of the cranial tibial shaft (Figs 5A, B, 6). The muscle passes across the cranial aspect of the ankle to insert to the plantar-medial tubercule of the base of metatarsal II (Fig 7) and acts to dorsiflex and invert of the pes.

Reflecting the relative length of the tibia, the origin is relatively shorter in *M. irma* (proximal quarter of the tibia shaft) and *M. fuliginosus* (proximal one fifth of tibial shaft). Tendon passed obliquely over the lower ankle joint and inserts onto the fascia covering the medial cuneiform (tarsal I) and the proximomedial aspect of the fourth metatarsal. An insertion to metatarsal IV was also noted for *M. giganteus* (Hopwood & Butterfield 1990), though more distally to the head of that bone, as well as to the base of metatarsal II. In *S. brachyurus* the origin was restricted to the proximal third of the tibial fossa (proximal one eighth of the tibia).

M. extensor digitorum longus (EDL)

M. EDL of digits II and III was a small, superficial muscle from the proximolateral aspect of the tibia, immediately below the epiphyseal line (Figs 5A, 6). A single tendon from the proximal third of the leg passed through a retinaculum deep to the other digital extensors to insert to digits II and III. The thin tendon divided at the level of the middle phalanges, one for each toe, and inserted to the dorsal aspect of the base of the distal phalanx. The tendon to the II and III digits has an especially deep retinaculum, separate from the two larger tendons. The

arrangement of the EDL is similar in *S. brachyurus*. This muscle is very small in the *M. irma,* with the tendon from proximal fifth of the tibia only.

M. EDL of digit IV arose from the cranial aspect of the head of the fibula and proximal two-thirds of tibia (Figs 5A, 6). The aponeurotic fibres blended into the dorsal fascia of the proximal phalanx, together EDL IV and V, to form strong insertions to the bases of the proximal and distal phalanges of digit IV. The fleshy belly of this muscle extends along the proximal two-thirds of tibia in *D. lumholtzi*; in *M. irma* the fleshy portion is only on the first third of the tibia. In *S. brachyurus* the origin was from the caudo-lateral aspect of the lateral tibial condyle rather than the fibular head. A femoral origin has been reported for *Petrogale* (Parsons 1896) and *M. rufus* (Windle & Parsons 1898), but not in *M. giganteus* (Hopwood & Butterfield 1990).

M. EDL of digits IV and V arose from the cranial aspect of the head and proximal fifth of the cranial border of the fibula, and the interosseous membrane (Fig 5A). The tendon split to insert to the distal phalanx V and a tendon to the dorsal fascia of digit IV. Origin in *M. irma* from proximal half of fibula. Origin in *M. fuliginosus* origin from the cranial fibula, and small portion of the tibia, immediately distal to the extensor of digit IV; insertion traced to the distal phalanx of digit V only. In *S. brachyurus* the origin was from the caudo-lateral aspect of the tibia below the lateral condyle rather than from the fibula.

As a group, these muscles extend the phalanges and dorsiflex the foot. A strong retinaculum holds the tendons of the extensor muscles on the dorsal aspect at the level of the lower ankle joint. In *S. brachyurus* the tendons of insertion do not merge as observed in *Macopus;* the EDL IV inserted to the medial side of the toe, and the EDL IV and V inserted to the lateral side.

Lateral leg

M. fibularis [peroneus] longus et brevis

M. fibularis longus et brevis originated from the lateral aspect of the head and shaft of the fibula (Figs 5A, B). Its tendon passed under the tendon of the lateral digital extensor to insert deeply to the dorso-lateral aspect of the base of the fifth metatarsal (Fig 6). It acts to dorsiflex and evert the pes.

The tendon was relatively thick in *D. lumholtzi* in comparison to other macropods. The fleshy belly extended along the proximal third of the crus in *D. lumholtzi*; but was limited to the proximal quarter of the crus in *M. irma* and the proximal tenth in *S. brachyurus*. In *M. fuliginosus* the origin was from the head of the fibula only. Carlsson (1915) described four muscles of the peroneus group in *H. moschatus*. Hopwood and Butterfield (1990) described three muscles in *M. giganteus*, with a common origin from the head and proximal surface of the fibula, with insertions to tarsal I, digit IV and digit V.

M. extensor digitorum lateralis

M. extensor digitorum lateralis originates from the lateral aspect of the mid fibula (Figs 5B, C). The tendon passed under extensor retinaculum and behind the lateral malleolus to insert to the lateral aspect of the base of the middle phalanx V (Fig 6). The muscle acts to extend and abduct digit V and also dorsiflexes the talocrural joint.

The origin of this muscle in *M. irma* and *S. brachyurus* was from the proximal third of the lateral fibular shaft. In *M. fuliginosus* the origin was from the proximal quarter of the lateral aspect of the fibula. This muscle seems to correspond to the m. peroneus digit V described for *M. giganteus* (Hopwood & Butterfield 1990).

An additional very tiny muscle with long tendon was found on lateral aspect of the EDL in *D. lumholtzi*; we were unable to trace it to its insertion. It may have been the M. extensor hallucis brevis mentioned in *D. dorianus* (Carlsson 1915).

Caudal leg

M. triceps surae

M. gastrocnemius medial head arose from the medial supracondylar fossa of the femur (Figs 3C, 7). The lateral head arose via thick aponeurotic fibres from the lateral epicondyle and the fascia of the knee and patelloid (Figs 3B, 6).

M. soleus lay on the deep surface of the lateral gastrocneumius; arising from the ligament of the sesamoid of the superficial digital flexor. The three portions insert to the calcaneal tuberosity via the common calcaneal tendon and act to plantarflex the pes.

In *D. lumholtzi* the fleshy portion of the gastrocnemius was on the proximal two-thirds of the length of the tibia and the tendon was relatively short and inserted to the lateral aspect of the calcaneal tuberosity. In *M. irma* the origin of the lateral head was from the lateral supracondylar ridge; medial head from the distal aspect of the medial supracondylar fossa. In *M. giganteus*, the lateral head is attached to the lateral epicondyle of the femur (Lodder 1991). In *M. fuliginosus* the origin was more obviously from the fascia of the patelloid than the epicondyle of the femur. In *S. brachyurus* we observed an aponeurotic connection to the medial aspect of the crest of the tibia. In *Aepyprymnus*, the lateral head is attached to the patelloid the tibia and fibula and to the lateral epicondyle (Lodder 1991). The soleus was more completely separable from gastrocnemius in *D. lumholtzi*; conjoined at origin from sesamoid, but distinct belly. In *M. irma* the soleus was incompletely separable from the lateral gastrocnemius; distinct origin, but conjoined distally. Hopwood and Butterfield (1990) note a possible remnant of the soleus in *M. giganteus* in association with the lateral head of the gastrocnemius. The muscle was described as absent in *Petrogale* (Parsons 1896).

M. flexor digitorum superficialis (m. plantaris)

M. flexor digitorum superficialis took its origin from the lateral epicondyle of the femur via a thick tendon with an internal sesamoid bone (lateral fabella) (Figs 3B, C). The broad, thick tendon passes over the calcaneal tuberosity and along the plantar aspect of the pes (Figs 6, 7). The tendon split at the level of the calcaneal-cuboid articulation to insert to digits IV and V. Digit IV had a large tendon to the base of the middle phalanx and a smaller tendon to the lateral aspect of the base of the middle phalanx of digit V. The tendon to digit IV was perforated by the deep flexor tendon; the tendon to digit V was not perforated, but passed laterally to the deep flexor tendon. A thick retinaculum covered the tendon over the proximal half of the base of the proximal phalanx. This muscle acts to plantarflex the digits and talocrural joint.

In *D. lumholtzi* the fleshy belly extended almost the entire length of the tibia, converging to a short, thick tendon immediately before its attachment to the calcaneal tuberosity. In *M. irma* and *M. fuliginosus* the fleshy belly gave rise to the tendon in the proximal half of the crus. The sole of the foot was very fatty; the tendons of the superficial digital flexor were embedded within the fatty pad. It was interesting that while the superficial flexor tendon to the fourth toe was perforated by the deep digital flexor tendon, as is typical in other mammals, the tendon to the fifth toe was not. Rather it inserted laterally on the fifth toe only. This arrangement was noted in all the specimens we observed.

M. flexor digitorum profundus (m. flexor digitorum longus)

M. flexor digitorum profundus originated from the head of the fibula, proximal third of the caudal aspect of the fibula, the interosseous membrane, mid-caudal shaft of tibia, below m. popliteus and a small portion from the lateral condyle of the tibia (Figs 5B, C). The short, thick tendon passed along the medial aspect of the calcaneus, through the plantar groove of the cuboid, to insert to the base of the distal phalanx of each digit (II, III, IV, V) (Figs 7, 8). The thick tendon separated into two at the calcaneal-cuboid joint on the sole of the foot; one tendon to digits II and III; the other to digits IV and V. The very thin tendons for digits II and

III remained combined until immediately before their insertion. The tendons to digits IV and V separated mid-length along the metatarsals. A retinaculum held each tendon in place at the level of the metatarsal head. The relative thickness of the tendons reflected the relative size of the digits.

The muscle covered the distal half of the tibia and was fleshy for almost the entire length of the crus. The proximal origin was very tightly bound to the popliteus. In *M. irma* the aponeurotic and fleshy origin was from the caudal aspect of the proximal half of the fibula and tibia (flexor fossa), from the fibrous interosseous membrane, and from the fascia of the popliteus. In *M. fuliginosus* the origin was from the proximal two-fifths of caudal tibia (flexor fossa), fibula and interosseous membrane, and the lateral aspect of the head of the fibula. *S. brachyurus* was similar to *M. irma*.

M. tibialis caudalis

M. tibialis caudalis was a small, short muscle belly from the surface of the popliteus. Its insertion was to the proximoventral tubercle of the medial trochlear crest of the talus. This muscle acts as a plantarflexor of the talocrural joint.

This muscle was not observed as a distinct portion in the other macropodines we dissected. This muscle was not mentioned in the description of *D. dorianus* (Carlsson 1914) and was not recorded in *M. giganteus* (Hopwood and Butterfield 1990).

M. popliteus

M. popliteus arose from the intercondylar fossa of the femur and inserted to the proximal two-fifths of the caudolateral aspect of the tibia including the tibial condyles, proximal two-fifths of fibula including the head of the fibula, and the interosseous membrane (Figs 3C, 5B, C, 7). The muscle fills deep caudal depression between the tibia and fibula and is triangular in

section. The popliteus would contribute to flexion of the knee and medial rotation of the tibia relative to the femur.

In *M. irma* the origin extended onto the disto-lateral fossa on the lateral epicondyle of the femur; the insertion was to proximal fifth of the caudal aspect of the tibia and proximal medial sixth of the fibula. In *M. fuliginosus* there was also an attachment to the medial aspect of the head of the fibula. Varied descriptions of this muscle, including the distinction of m. rotator fibulae have been recorded including *Petrogale* (Parsons 1896), *M. rufus* (Windle & Parsons 1898) and *H. moschatus* (Carlsson 1915).

Plantar pes

M. flexor digiti IV brevis

M. flexor digiti IV brevis was identified as a short fleshy muscle from the tendon of the deep digital flexor at the level of the mid-calcaneus gave a thin tendon to the fourth toe, deep to the superficial flexor tendon (Fig 8). The short tendon passed to insert into the deep ventral fascia of the fourth toe.

Mm. lumbricales

Two large and flattened superficial muscles of the pes observed after the removal of the superficial digital flexor where classified as mm. lumbricales (Fig 8). A medial lumbrical originated from the deep flexor tendon at the separation between the tendon of the digits II and III and the tendon of digit IV; distally at the level of the calcaneus and passing to the metatarsophalangeal joint. The lateral lumbrical originated from the deep flexor tendon at the split between the tendons of digits IV and V. The thin tendons passed in the fascia at the base of the fourth digit. Hopwood and Butterfield (1990) describe these muscles as lumbricals in *M. giganteus*.

Mm. flexores and adductores digiti

Deep to the tendon of the flexor digitorum profundis there was a dense mass of muscles; however the state of preservation of our specimen did not allow clear separation (Fig 8). The superficial layer of muscles appeared to arise from the plantar ligaments. Carlsson (1915) reported that typically two or three lumbricals are retained in the Macropodidae, although they were missing in *H. moschatus*. The deep layer comprised a number of interconnected short muscle fibres that passed to the phalanges (*mm. flexores and adductors digiti*) and filled the uneven spaces between the metatarsals (*mm. interossei*). This muscle mass included an abductor of the fifth toe which inserted to the medial aspect of the proximal phalanx of the fifth digit. A portion also appeared to originate from caudal plantar sesamoid bone at the level of the base of the fourth metatarsal. This group of muscles was much larger and more obvious in *D. lumholtzi* than in the other macropods examined.

Discussion

The hind limb musculature anatomy of the tree-kangaroos differed from that of terrestrial macropodines in a number of ways that appeared to be functionally related to locomotion within an arboreal environment. Firstly, the muscles of the hind limb of *D. lumholtzi* had a greater degree of differentiation, in that they were either more clearly separable from associated muscles or more highly subdivided internally. This was true of individual muscles and entire muscle groups. The m. gluteofemoralis comprised three distinct portions rather than the usual two. The two bellies of the gluteus medius and portions of the adductor muscles both had two distinct and separate origins from the pelvis. Within the crus, the digital extensor muscles and lateral muscles of the leg were much more readily separable into individual muscles, and a distinct m. tibialis caudalis was identified. A much greater number of intrinsic muscles were observed within the pes. Anapol and Barry (1996) similarly found greater internal differentiation in arboreal *versus* semi-terrestrial guenons (*Cercopithecus* spp.), particularly in the thigh, and took this to indicate reduced division of labour for terrestrial gaits. Thus, the greater differentiation of muscles within the hind limb of

Dendrolagus suggests a much greater range and dexterity in the movements within the individual joints and regions of the hind limb. This in turn may reflect the greater diversity of movements and manoeuvrability of the hind limb in tree-kangaroos, and correspond with the more variable and flexible nature of the arboreal habitat in comparison to the relatively constant terrestrial environment.

Secondly, within the tree-kangaroo hind limb, and particularly within the crus, many muscles had relatively longer fleshy bellies, with longer, more distally extending origins and very short, stout tendons of insertion. This was true of all of the muscles of the leg which typically (in other macropodines) insert with relatively very long tendons: the triceps surae (mm. gastrocnemii and soleus), the pedal flexors and extensors and the fibularis muscle group. As noted by Hopwood and Butterfield (1990), the bellies of the crural muscles of *M. giganteus* are restricted to the proximal half of the crus, with long tendons enabling the insertion to the pes. In contrast, in *D. lumholtzi*, the bellies of the crural muscles all reached greater than half the length of the crus and in most cases over three-quarters the length of the crus. Indeed, the superficial and deep digital flexor muscles converged to a tendon only immediately before entering the pes. Typically, the long tendons of gastrocnemius and superficial digital flexor scale with positive allometry with increased size in macropodoids (McGowan, Skinner *et al.* 2008). Functionally the long tendons of these muscles are important for locomotor efficiency by acting to store and then return elastic energy during continuous bipedal bounding (Alexander and Vernon 1975). Our observations suggest that the tendons of these muscles in tree-kangaroos would not scale with the terrestrial macropodoids examined by McGowan et al. (2008). The greatly reduced length of tendons in tree-kangaroos would lessen the role of tendon functioning for elastic energy storage. Instead, these muscles in tree-kangaroos are likely to function for a much greater degree of joint control which would be highly advantageous for movement along uneven and flexible branches.

Thirdly, in *D. lumholtzi*, some of the muscles that are important for providing stability or propulsion had a modified arrangement of their bony attachments that enhance mechanical advantage. In particular, the m. pectineus and m. gluteofemoralis had more distally positioned insertions to the femur. The more distally placed insertion functionally would result in an improved mechanical advantage by increasing the length of the in-lever arm. The relatively shorter limb segments in tree-kangaroos and, in particular, the relatively reduced length of the pes, would provide a further mechanical advantage through a reduced length of the out-lever arm in comparison to terrestrial macropodines. The improved mechanical advantage of the m. pectineus would support the function of the enlarged adductor mass for strong adduction of the hind limb during climbing. The improved mechanical advantage of the m. gluteofemoralis would contribute to extension of the hip.

Fourthly, the relative size and development of the deep muscles of the hip in *D. lumholtzi* was different from that of the terrestrial macropods. The bony attachments of the gluteus minimus, external obturator, gemelli and quadratus femoris muscles were somewhat differentin *D. lumholtzi*. It seems likely that this may reflect an important role of the deep rotator muscles of the hip for improved manoeuvrability. The origin of the gluteus minimus muscle was more compact, arising from the base of the ilium in *D. lumholtzi*, in comparison to *M. irma*, *M. fuliginosus* and *S. brachyurus* where the origin extended along the entire lateral edge of the ilium, alongside the gluteal fossa. The insertion in each terrestrial species was also longer than in *D. lumholtzi*, along an arc from the craniomedial aspect and along the craniolateral line of the greater trochanter. The elongate origin of the gluteus minimus in the terrestrial macropodines would contribute to greater mechanical advantage for hip extension. The more localised bony attachments in *D. lumholtzi* may also allow this muscle more discrete actions on a finer scale of movement in tree-kangaroos, rather than contributing to broad actions of large hip extensor groups in terrestrial macropodines. The gluteus minimus muscle of *D. lumholtzi* was better arranged to have a discrete action of medial rotation of the femur at the

hip joint, and thus enhance dexterity of the hind limb, in comparison to that of terrestrial macropodines.

Finally, while detailed analysis of comparative quantitative muscle parameters was not undertaken in this study, there were apparent differences in the relative size of hind limb muscles between tree-kangaroos and terrestrial macropodines that are suggestive of possible physiological adaptation of the limb musculature of tree-kangaroos for arboreality. The mm. adductores appeared to be relatively large which seems likely to reflect strong adduction of the hindlimbs against tree trunks or branches during climbing. In *D. lumholtzi*, the m. quadratus femoris (which does not cross the knee) appeared relatively large while the m. biceps femoris appeared relatively small. This diversion from the proportions more typically seen in terrestrial macropodines suggest that hip extension in tree-kangaroos occurs with less emphasis on simultaneous extension of the knee. This would correlate with known differences in the gait of tree-kangaroos, at least some of which utilise a shuffling, alternate use of the flexed hind limbs, in comparison to terrestrial macropodines where limb extension for leaping is more important (Windsor and Dagg 1971). In contrast, it has been suggested that hopping in terrestrial macropodines relies on a greater emphasis on the extensor muscles in the pelvic limb, particularly that act across both the hip and knee joints (Hopwood & Butterfield 1990). The mm. quadriceps group (in particular the m. vastus lateralis) appeared relatively smaller in *D. lumholtzi* in comparison to *M. irma,* which is further suggestive of the maintenance of a much more flexed knee during locomotion in tree-kangaroos. This observation agrees with findings in other arboreal groups, for example primates (Schmitt 2003; Schmidt 2005b), where a more flexed limb posture has been shown to result in greater stability during climbing by lowering the centre of mass (Cartmill 1985).

It is of interest to note that *S. brachyurus* was different in some respects to both *M. irma*, *M. fuliginosus* and *D. lumholtzi.* When moving at slower speeds, *S. brachyurus* employs a quadrupedal bounding gait (Windsor and Dagg 1971), similar to that observed in some

Dendrolagus spp., while at faster speeds quokkas utilise the more typical macropodine bipedal hop. Anatomical differences were observed in the arrangement of the m. gluteofemoralis, mm. gemelli, m. gluteus medius, and the m. extensor digitorum longus. In some instances, similarities between *S. brachyurus* and *D. lumholtzi* may reflect the slower speed and more flexed posture of the knee during locomotion in *S. brachyurus*. It is also possible that the anatomy of *S. brachyurus* reflects a more plesiomorphic condition for this group. *S. brachyurus* apparently diverged from the macropodine lineage earlier than the other genera investigated here (Prideaux and Warburton 2010); however, additional data are required from more basal groups of macropods to test this hypothesis.

Overall, the pattern of observed differences between *D. lumholtzi* and terrestrial macropodines, exemplified by the species of *Macropus,* are essentially comparable to the muscular variation that has been described for other groups of terrestrial versus arboreal mammals. The differences between the species in this study can be related to generalised principles that reflect the constraints imposed by the different physical and mechanical properties of arboreal versus terrestrial substrates. However, the differences between tree-kangaroos and terrestrial macropodines are less extreme in nature than would be generally expected between arboreal and terrestrial members of a group. Tree-kangaroos, uniquely, evolved from bipedal, saltatorial ancestors. This evidently imposed much greater adaptive constraint on the morphology of tree-kangaroos than has occurred in many other arboreal mammal groups.

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Figure captions

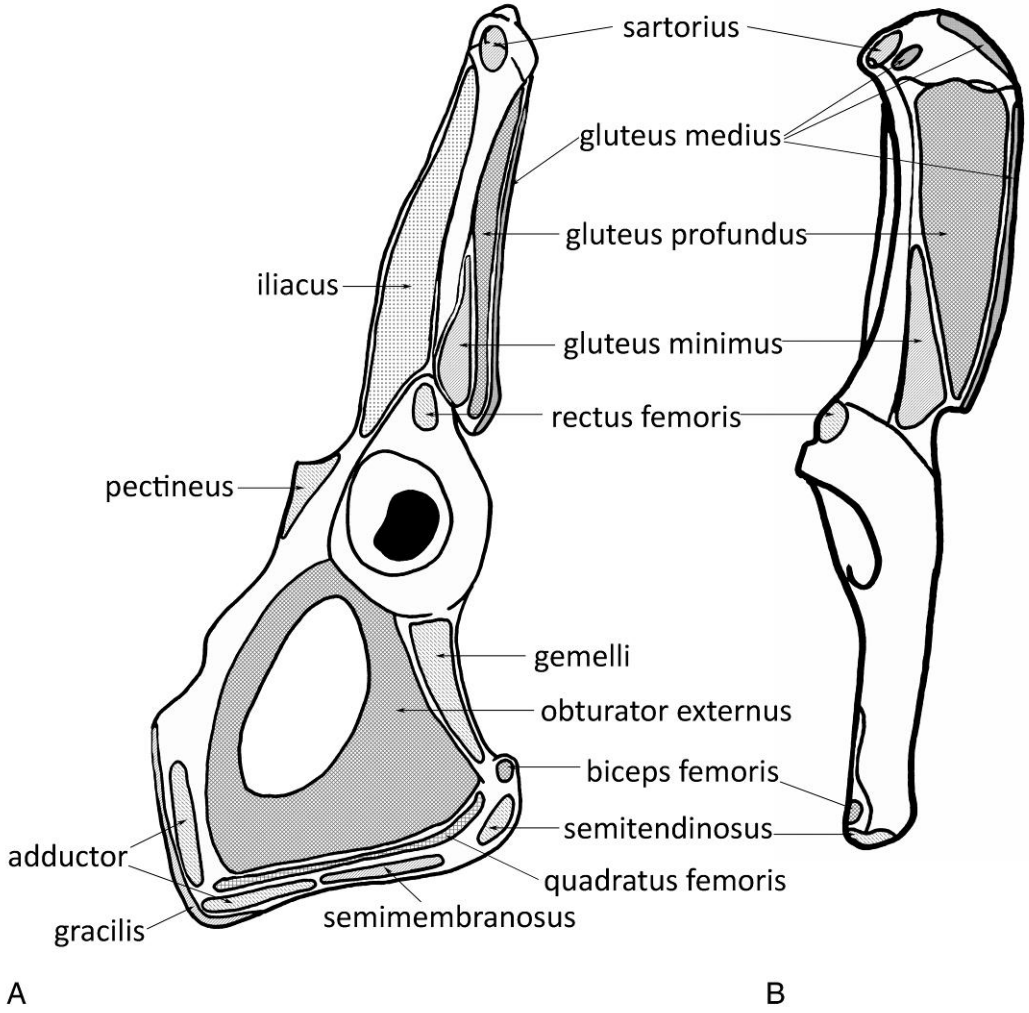

Figure 1 - Left os coxa (innominate) of *Dendrolagus lumholtzi* showing areas of muscle origin and insertion. A, ventrolateral view; B, dorsolateral view.

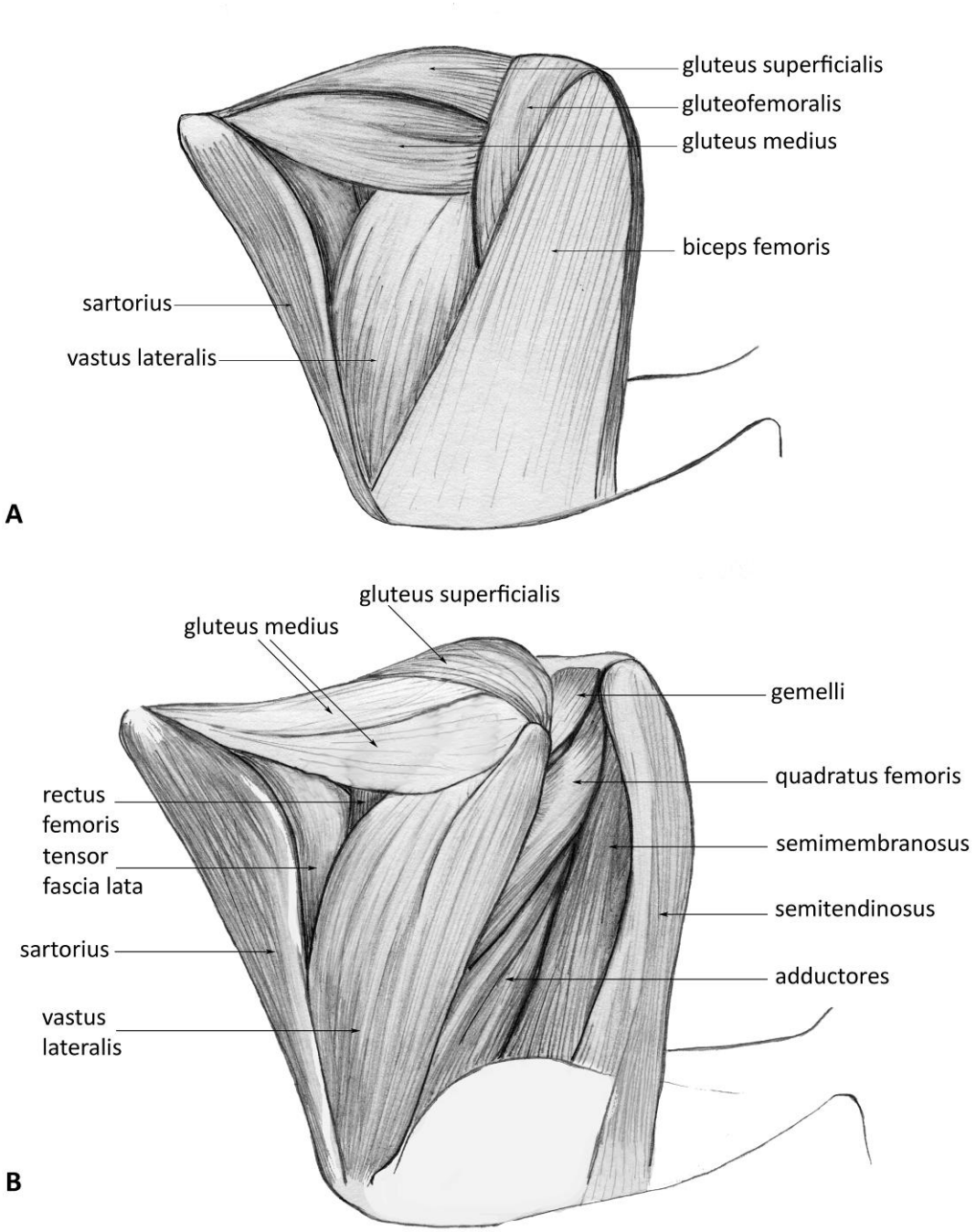

Figure 2 - Muscles of the lateral hip and thigh of *Dendrolagus lumholtzi* (left), A superficial muscles, B deep muscles (after removal of gluteal muscle group and biceps femoris).

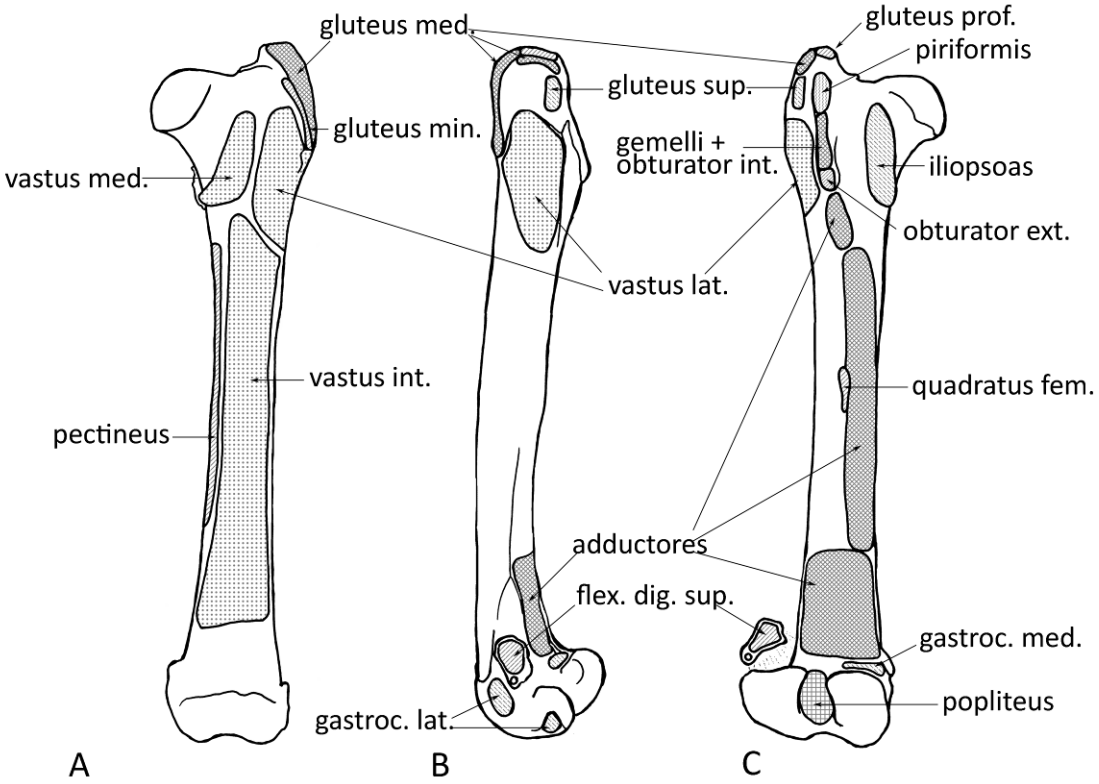

Figure 3 – Left femur of *Dendrolagus lumholtzi* showing areas of muscle origin and insertion. A, cranial view; B, lateral view; C, caudal view.

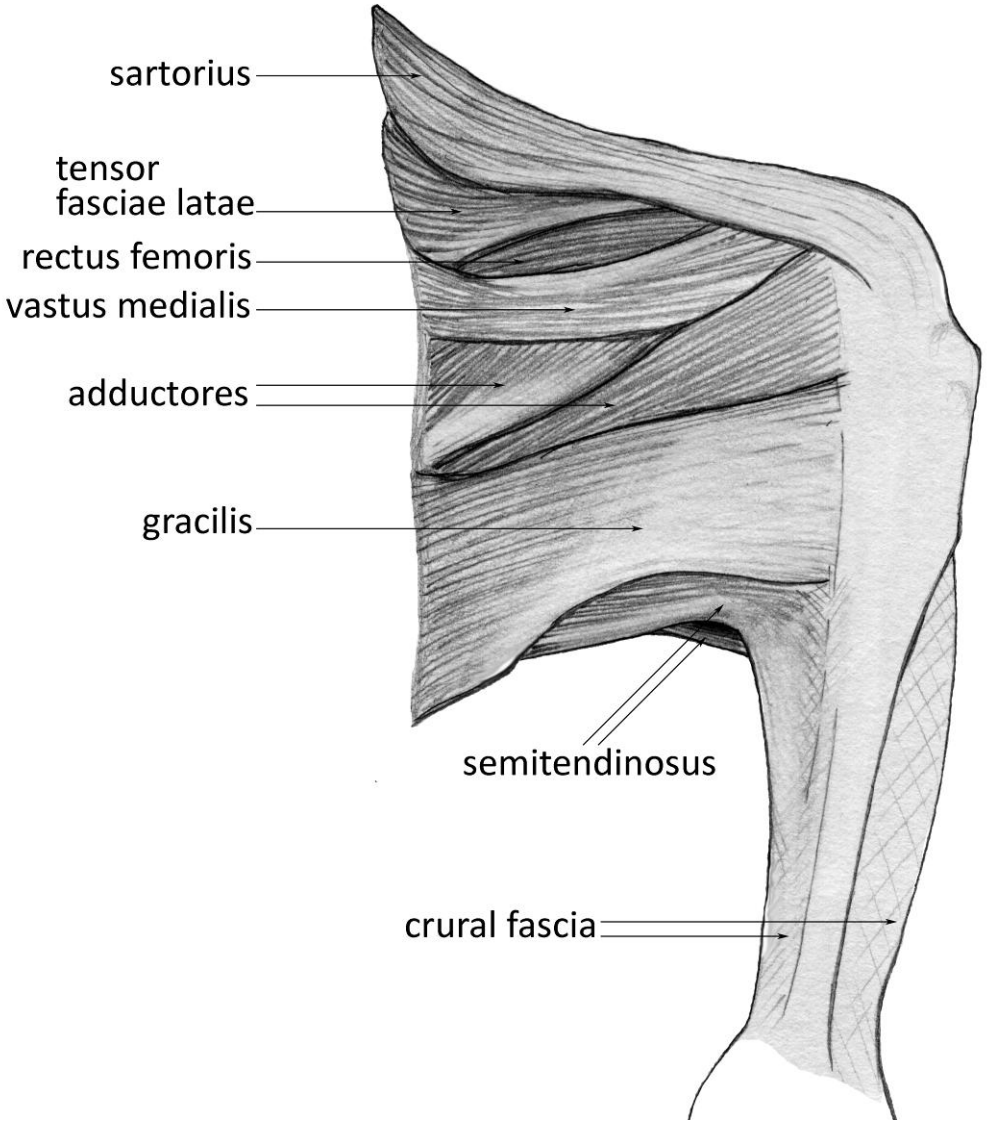

Figure 4 - Superficial muscles of the medial thigh of *Dendrolagus lumholtzi* (left).

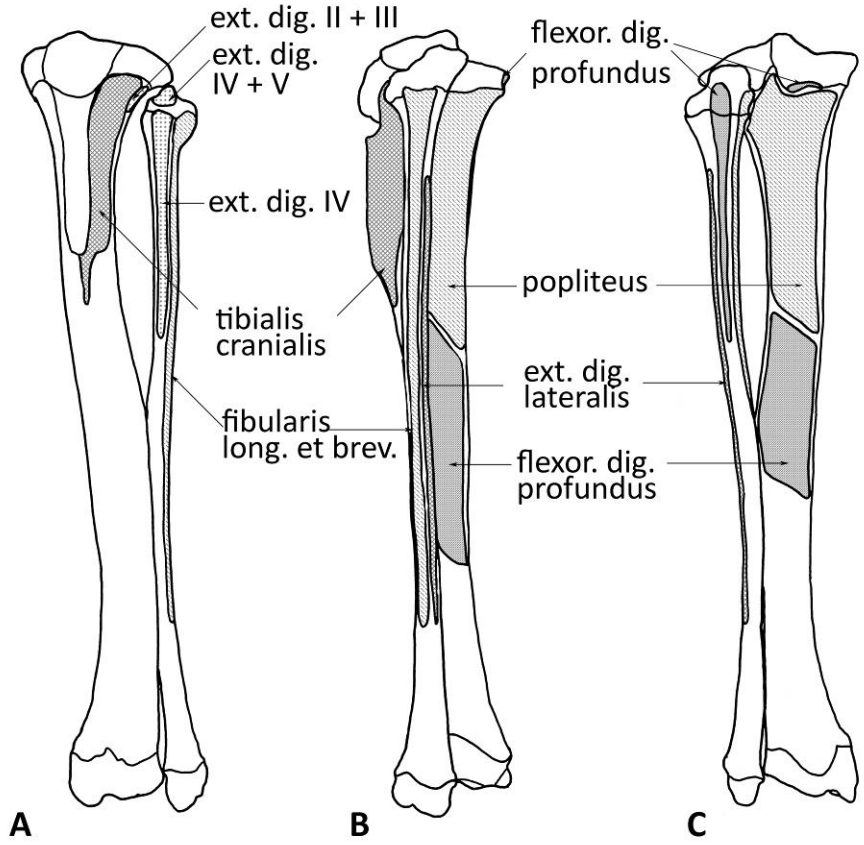

Figure 5 - Left tibia and fibula of *Dendrolagus lumholtzi* showing areas of muscle origin and insertion. A, cranial view; B, lateral view; C, caudal view.

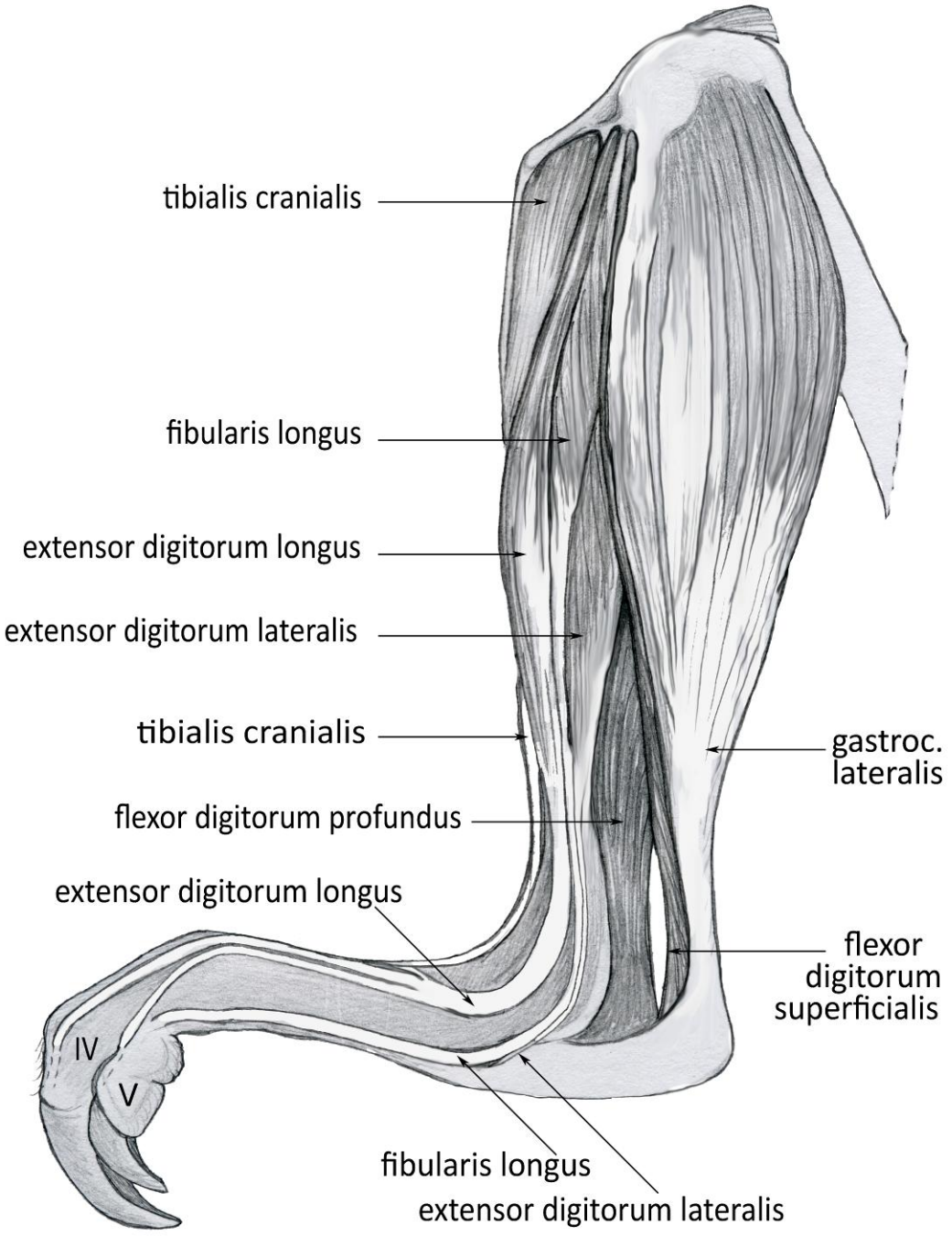

Figure 6 - Muscles of the lateral leg of *Dendrolagus lumholtzi* (left).

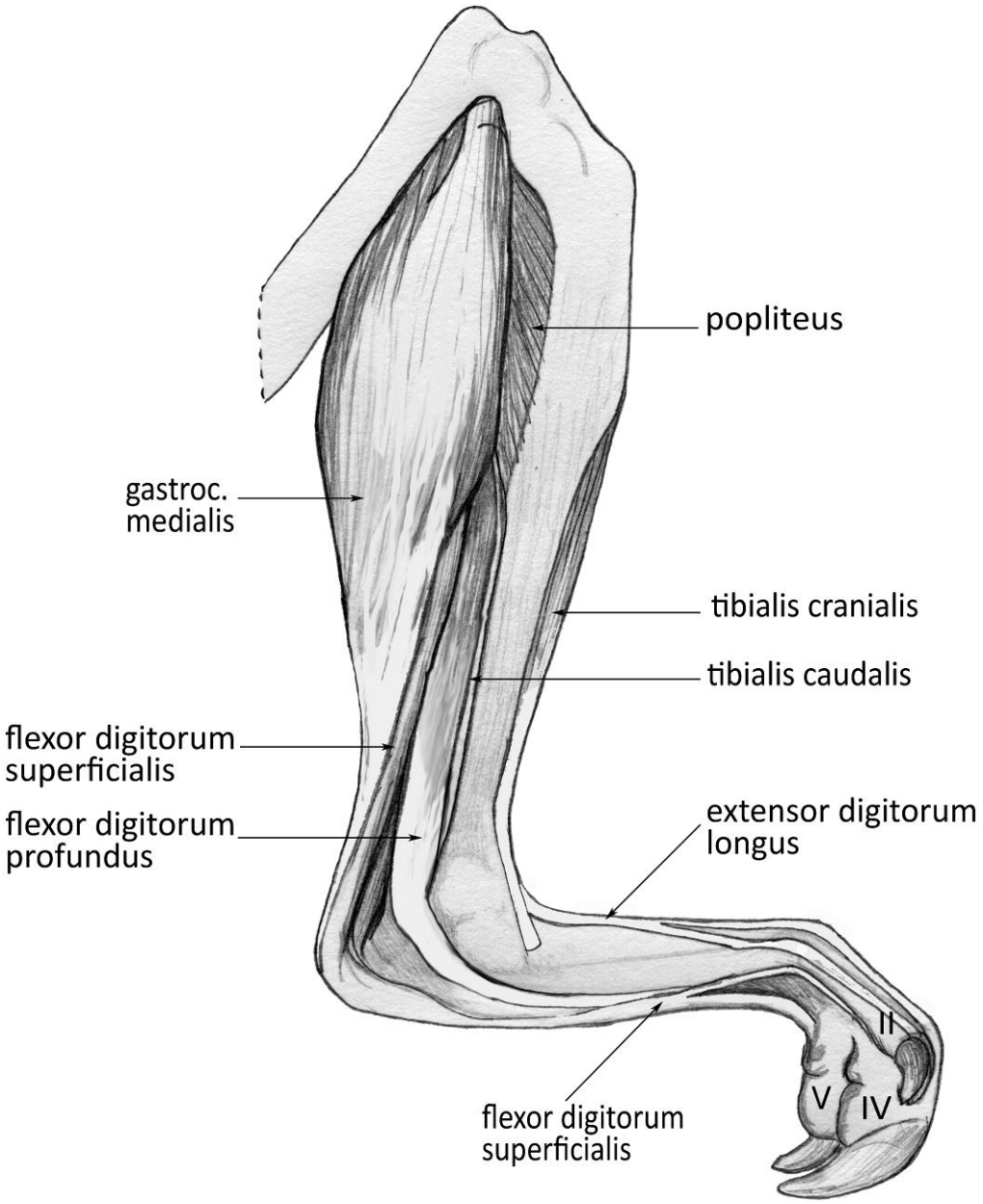

Figure 7 - Muscles of the medial leg of *Dendrolagus lumholtzi* (left).

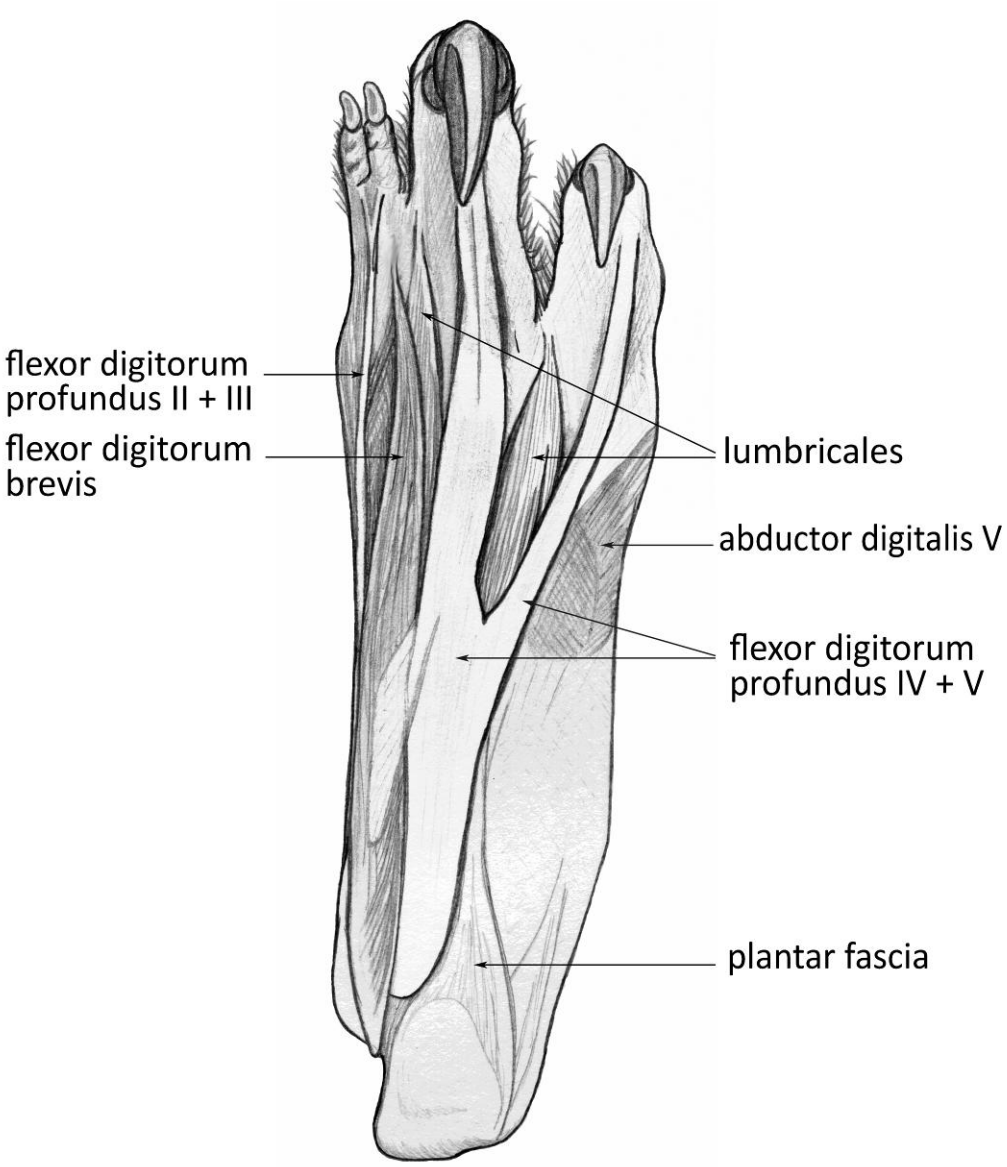

Figure 8 - Intrinsic muscles of the plantar aspect of the pes of *Dendrolagus lumholtzi* (left; tendons of the m. flexor digitorum superficialis have been removed).